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1	Future climate and land-use intensification modify arthropod community
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26 Abstract

27 Climate change and land-use intensification pose increasing threats to biodiversity, with 28 climate change expected to eventually surpass other global environmental change drivers and 29 become the greatest threat to biodiversity in the future. Understanding the combined ecological impacts of multiple global change drivers is crucial to predict future scenarios of 30 31 biodiversity change. However, experimental evidence for the impacts of land-use intensification under current and future climate scenarios is lacking, even though this is 32 imperative for understanding future trajectories of biodiversity in agricultural landscapes. We 33 34 experimentally tested for the simultaneous effects of land-use intensification and climate change on arthropod biodiversity in a field-scale grassland experiment known as the Global 35 Change Experimental Facility (GCEF). Specifically, we tested whether future scenarios of 36 37 climate change are likely to exacerbate impacts of land-use intensification on arthropod diversity and abundance across different trophic levels by sampling aboveground arthropod 38 communities in low and high land-use intensity grasslands under current and future climatic 39 conditions. We found that climate change reduced total abundances of arthropods and 40 increased evenness of the whole community, while only having trophic level-specific effects 41 42 on detritivore abundance and evenness. Land-use intensification reduced abundance of the 43 whole community, predators and detritivores, but only eroded species richness of the whole 44 community and herbivores, with the magnitude of declines in predator and detritivore 45 abundance depending on the climate scenario. Additionally, both land-use intensification and climate altered species composition of the whole community and within the predator, 46 47 herbivore, and detritivore trophic levels. We show that climate change and land use 48 intensification cause simultaneous shifts in arthropod abundance, species richness, and 49 species composition across trophic levels. Changes in arthropod communities as a result of

50 climate change and land-use intensification will likely have profound consequences for

51 ecosystem functioning under future environmental conditions.

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Keywords: Agricultural intensification, climate change, drought, insects, invertebrates, landuse change, grassland, warming

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57 **1. Introduction**

Multiple drivers of environmental change pose increasingly significant threats to biodiversity 58 (Fischer et al., 2018; Sala et al., 2000; Vitousek, 1994). Land-use intensification, in 59 particular, is considered to be one of the largest of these threats (Fischer et al., 2018) due to 60 its widespread and dramatic impacts on biodiversity at local and landscape scales (Ekroos et 61 al., 2020; Gossner et al., 2016; Newbold et al., 2015). In grassland ecosystems, processes 62 63 such as harvesting, and input of fertilizers play a particularly strong role in reducing arthropod abundance and diversity (Ekroos et al., 2020; Humbert et al., 2010). Grasslands 64 cover approximately 30% of the Earth's land surface and are critical for delivering a wide 65 range of ecosystem services, including forage production for livestock, carbon sequestration, 66 and biodiversity conservation (Bengtsson et al., 2019; Pilgrim et al., 2010). While land-use 67 intensification may currently pose the greatest and most acute environmental threats to 68 grasslands, climate change is expected to eventually surpass other global environmental 69 change drivers and become the greatest threat to biodiversity in the future (Millennium 70 Ecosystem Assessment, 2005). 71

72 In this century, mean surface temperatures are expected to increase by at least 1.5 °C 73 to 4.8 °C compared to preindustrial levels as a result of human activities, depending on greenhouse gas concentrations in the atmosphere (IPCC, 2014). Shifts in global precipitation 74 75 regimes are also expected which, in combination with warming, will lead to more frequent drought events and continue to intensify threats to global biodiversity (Tilman and El Haddi, 76 1992). These global change drivers, however, are unlikely to have independent effects on 77 78 ecosystems. Instead, it is crucial to consider interactions between global change effects, such as climate change and land-use, to understand the synergistic or antagonistic effects these 79 80 drivers may have on ecological communities (Binzer et al., 2016; Oliver and Morecroft, 2014). Indeed, the combination of changing climate with land-use intensification could 81 potentially explain the suspected dramatic decline in insect abundance over the last decades, 82 83 but experimental evidence is crucial to identify the drivers of these observed changes in 84 arthropod densities (Dormann et al., 2008; Hallmann et al., 2017; Soroye et al., 2020).

Abundance, diversity, and composition are important characteristics that collectively 85 describe different aspects of community structure and are all strongly linked to ecosystem 86 functioning (Barnes et al., 2018; Hooper et al., 2005; Soliveres et al., 2016). These 87 88 components can therefore be used as indicators of ecosystem responses to global 89 environmental changes. Changes in diversity, namely whether certain species are entirely 90 extirpated from a system or the relative dominance of species changes in response to 91 environmental stress, can be determined by quantifying species richness and evenness, 92 respectively. Diverse and abundant arthropod communities provide a variety of ecosystem 93 functions that contribute to the supply of ecosystem services and are therefore highly 94 beneficial for humans (Cardinale et al., 2012; Chapin III et al., 2000). These include 95 processes regulating food security or soil fertility through pollination, natural pest control, and decomposition (Altieri, 1999; Barnes et al., 2020; Doran and Zeiss, 2000; Kremen et al., 96

2007; von Berg et al., 2009), which may be under threat as arthropod communities respond to
multiple environmental change drivers.

99 Recent studies have documented alarming declines of arthropods over the past 100 decades (Hallmann et al., 2017; Leather, 2018; Seibold et al., 2019; van Klink et al., 2020), though there is still considerable debate over the validity and generality of these worrying 101 102 trends (e.g. Crosslev et al., 2020). There is considerable evidence from space-for-time studies and time-series studies that arthropod declines are linked to land-use intensification, 103 (including shifts in habitat structure, plant-diversity and fertilizer use) and also some 104 105 evidence for negative impacts of climate change (Dormann et al., 2008; Ekroos et al., 2020; Gossner et al., 2016; Hendrickx et al., 2007; Seibold et al., 2019). Additionally, organisms 106 from different trophic levels may respond differently to global change drivers (Dormann et 107 108 al., 2008) and thus the processes linked to these groups, such as decomposition or pestcontrol, may follow similar patterns. However, experimental tests of combined land-use 109 intensification and climate change impacts on arthropod communities are lacking. Due to the 110 highly complex nature of the direct and interactive impacts of these combined environmental 111 change drivers, it is inherently difficult to delineate clear hypotheses of how multitrophic 112 113 species assemblages will respond when they combine. Therefore, experimental studies that can isolate and identify the effects of these drivers and their interactions are imperative to 114 115 begin to understand the future consequences of these combined global change drivers for arthropod biodiversity. 116

To determine whether future scenarios of climate change are likely to exacerbate
impacts of land-use intensification on arthropod communities (Mantyka-Pringle et al., 2015;
Oliver and Morecroft, 2014) spanning multiple trophic levels, we test for responses in
abundance, species richness, species evenness and community composition to land-use
intensification under current and future climatic conditions. To do so, we use an agricultural

122 field-scale global change experimental facility in Germany (the GCEF; Schädler et al., 2019), to investigate the combined effects of climate change and land-use intensification on 123 grasslands by simulating a future climate change scenario under field conditions at different 124 levels of land-use intensification. We test for interactive effects of climate change and land-125 use intensification, whereby we expected land use impacts on invertebrate communities to be 126 exacerbated under the future climate scenario. We hypothesised that arthropod abundance, 127 128 species richness, and evenness would decline in intensively managed grasslands and under the future climate scenario. In particular, we expected that the simulated global change 129 130 drivers would affect species richness, evenness and species composition due to differential, trait-dependent responses of species (Simons et al., 2015). In that vein, we also expected that 131 the strength of these responses would vary among trophic levels due to their varying 132 133 sensitivities to environmental change drivers.

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135

136 2. Materials and Methods

137 **2.1 Study Site**

We used the experimental set-up of the Global Change Experimental Facility (GCEF) in Bad 138 Lauchstädt, Saxony-Anhalt, Germany. The area is characterized by sub-continental climate, 139 with a mean annual temperature of 9.7°C (1993–2013) and mean annual precipitation of 525 140 mm (1993–2013) (Schädler et al., 2019). The GCEF experiment started in 2014 and consists 141 142 of ten experimental units $(80 \times 24 \text{ m})$, where each is covered by a steel frame. Five of the experimental units are influenced by current climatic conditions where the steel frame only 143 serves as a control for climate manipulation. The remaining five units are influenced by a 144 145 future climate change treatment whereby the walls and roof are added to the steel frames and are closed overnight. In doing so, this effectively results in a passive temperature increase of the daily mean temperature by 0.55 °C and also manipulates precipitation patterns. In spring and autumn, the quantity of rain is artificially increased by ca. 10 % with irrigation, and the summer precipitation is reduced by ca. 20 %. The climate change treatment is based on the climatic conditions projected for central Germany in 2070-2100, based on different dynamical regional climate models (for details, see Schädler et al., 2019).

Within each of the current (control) and climate change manipulation units, we 152 utilized two different land-use intensity treatments applied on 16 x 24 m plots: i) low 153 154 intensity managed grasslands and ii) high intensity managed grassland (see Figure 1). While 155 both land-use treatments were managed by mowing to simulate harvesting, the two land-use treatments differed in their initial sown plant species richness, harvest regime, and fertilizer 156 157 use. The high intensity managed grassland plots had five sown grass species, were harvested four times per year (with the first harvest in April), and were moderately fertilized. In 158 contrast, the low intensity managed grassland had 56 plant species sown initially, were mown 159 two times per year (with the first harvest in June), and had no fertilizers applied (see Schädler 160 et al. (2019) for more details). 161

162

163 **2.2 Sampling and Species Identification**

In order to sample as many species as possible despite different phenologies across the
growing season, arthropods were sampled four times in total, in April, May, early July and
late July of 2017. We collected all aboveground arthropods in a 25 cm x 25 cm x 100 cm
sampling cage (0.25 m³ volume) using a suction sampler (EcoVac, ecoTech Umwelt
Meßsysteme). The entire cage was exhaustively sampled (i.e. ground vegetation and flying
arthropods) for approximately one minute until no more arthropods were visible in the cage,

which has been shown to be highly effective for sampling aboveground grassland arthropods
(Brook et al., 2008). Organisms were then stored in a cooling box for transport to the
laboratory where they were first stored at -20 °C and then transferred into 70 % ethanol.

173

174 **2.3 Species and trophic group identification**

All arthropods (excluding larval and pupal stages) were first sorted to order level, of which 175 five of the most abundant major taxonomic groups (Araneae, Auchenorrhyncha, Coleoptera, 176 177 Diptera, and Hymenoptera; see Table S1 in supporting information for a complete list of collected taxa) were further identified to family, genus, or species level when possible by 178 specialist taxonomists (see Acknowledgements). To quantify the effect of climate change and 179 180 land-use intensity on arthropod abundance and diversity, we quantified abundance as the accumulative sum of all individuals across the 4 temporal samples per cage, observed species 181 richness (i.e., the total number of unique species collected across the 4 temporal samples), 182 expected species richness using the jackknife2-estimator (accounting for possible 183 undersampling of the communities), and species evenness as response variables. Evenness 184 185 was calculated with the Evar index (Smith and Wilson, 1996), as this evenness index is independent of species richness. In order to quantify the changes in relative abundances and 186 composition of arthropod communities between the climate change and land-use intensity 187 188 treatments, we assessed the dissimilarity of communities among treatments using the "metaMDS" function from the vegan package using the Bray-Curtis Dissimilarity index. 189

In addition to the whole community response, we tested the effect of climate change
and land-use intensification on different trophic groups. Therefore, all individuals of the five
taxonomic groups were ascribed to trophic groups. The selected trophic groups were
predators (arthropods that consume or parasitize animals), herbivores (arthropods that

194 consume or parasitize plant tissues or fluids), omnivores (arthropods that feed on different trophic levels, such as animals, plant material or dead organic matter) and detritivores 195 (arthropods that consume dead organic matter). Literature was searched for ascribing trophic 196 197 groups to species, genus, family or orders of arthropods, with the highest possible taxonomic resolution (see Table S2 for more information). For analyses at both the whole-community 198 and trophic-group-level, only collected specimens that were identified to species were 199 200 included in analyses of species richness, evenness, and composition, whereas all specimens from the five most abundant taxonomic groups were included in analyses of arthropod 201 202 abundances.

203

204 2.4 Statistical Analysis

We used generalized linear mixed effects models (GLMM) with climate change, land-205 use intensification, and their interaction specified as fixed effects, along with experimental 206 207 block as a random effect (a random-intercept model, using the 'lme4' package in R). We modelled the responses of arthropod abundance and species richness to the global change 208 209 treatments on a Poisson error distribution, except where overdispersion was detected in which case we used a negative binomial error distribution. Species evenness was modelled on a 210 Gaussian error distribution and was log-transformed in order to meet the assumptions of 211 212 normality and ensure homoscedasticity of variance. We applied post hoc comparisons of estimated marginal means between climate treatments and between land-use intensity 213 treatments nested within climate treatments (using the 'emmeans' package in R) in order to 214 215 graphically highlight significant effects detected in the GLMMs.

To determine the effects of climate change and land-use intensification ondissimilarity in species composition, we applied a permutational multivariate analysis of

218 variance (PERMANOVA) using the 'adonis' function in the 'vegan' package, where we tested the effects of climate change and land-use intensification on the dissimilarity of 219 arthropod communities based on Bray-Curtis dissimilarity. For each model, we specified 220 221 'strata' as experimental block, to account for variation among blocks in the experimental design. Finally, where statistically significant effects of experimental treatments were 222 detected from the PERMANOVA, we conducted similarity percentages (SIMPER) analysis 223 using the 'simper' function to identify the set of species that contributed most to whole-224 community dissimilarity between the land use and climate treatments. All statistical analyses 225 226 were performed using R version 4.0.2 (R Core Team, 2020).

227

228 **3. Results**

We collected a total of 12,899 arthropods, of which 289 species were identified from the five 229 investigated taxonomic groups: Araneae (spiders; 1,037 individuals), Auchenorrhyncha 230 (leafhoppers; 2,640 individuals), Coleoptera (beetles; 2,137 individuals), Diptera (flies; 1,429 231 individuals), and Hymenoptera (2,640 individuals). The highest species number was found 232 233 for beetles with 141 species, followed by flies (84 species), spiders (30 species), leafhoppers (24 species), and Hymenoptera with 10 species and 95 families (some individuals from 234 Araneae, Auchenorrhyncha, Coleoptera, and Diptera could only be identified to the genus 235 236 level, and the majority of Hymenoptera were identified only to family level). Of the whole community, the 9,731 individuals that could be identified to species were categorized into 237 trophic groups. Herbivores were the most abundant group, with 4,551 individuals and 166 238 239 species. Predators were the second most abundant group with 2,750 individuals and 76 species, followed by omnivores with 1,705 individuals and 24 species. Detritivores were the 240

least abundant group in our sampling with 725 individuals and 23 species (see Table S2 formore details).

243

244 **3.1** Whole-community responses to climate change and land-use intensification

We found varying effects of climate change and land-use intensification on abundance, 245 species richness, and evenness of arthropod communities in the Global Change Experimental 246 Facility. The abundance of the whole arthropod community was negatively affected by both 247 248 climate change and land-use intensification. We found that total arthropod abundance was, on average, 20.1 % lower under future climatic conditions when compared to current climatic 249 conditions. We also found an even stronger decline in community abundance in response to 250 251 land-use intensification, with 37.5% lower average arthropod abundance in high versus lowintensity grassland plots. (Table 1; Figure 2A). In contrast to abundance, arthropod species 252 richness was significantly affected only by land-use intensity, for which we found an average 253 decline in mean species richness of 19.5 % with land-use intensification (Table 1, Figure 2B). 254 In addition to observed species richness, we found that expected species richness followed 255 256 the same response to land-use intensification (Figure S1). Community evenness was only significantly affected by climate change, where we found an average increase in evenness 257 from 0.48 (\pm 0.04 SD) under current climatic conditions to 0.56 (\pm 0.03 SD) under future 258 259 climatic conditions (Table 1, Figure 2C). As this result appeared rather counterintuitive, given that we expected certain species to perform better than others under future climatic 260 conditions (thus leading to reduced species evenness), we analyzed rank abundance curves 261 262 for both climate treatments to determine the cause of this positive response. These analyses revealed that the abundances of dominant species were strongly reduced with climate change 263

(Figure S2). This resulted in a more even distribution of abundance across species, hencenotable dominance by one or a few species was lower in the future climate treatments.

266

267 **3.2 Effects of climate change and land-use intensification on trophic groups**

We tested how climate change and land-use intensity affect abundance, species richness, and 268 evenness of four major trophic groups found in aboveground central European grassland 269 arthropod communities: predators, herbivores, omnivores and detritivores. Consistent with 270 271 the whole arthropod community, we found that the abundance of predatory arthropods decreased with land-use intensification. From the low to high-intensity land-use treatments, 272 predator community abundance decreased by 45.2 % under current climatic, which was 273 274 stronger than the 32.5 % decline under future climatic conditions (Table 2, Figure 3A). This diminished response to land use under future climatic conditions was supported by a 275 significant interaction between climate and land-use intensity (Table 2, Figure 3A). We did 276 not detect an effect of climate change and land-use intensification on abundance of 277 herbivores (but a trend toward declining abundance under intensive land use and future 278 279 climate) and there was similarly no discernible effect of the global change treatments on the community structure of omnivores (Table 2, Figure 3C). In contrast, detritivores were the 280 only group where we found a significant main effect of climate change on abundance, 281 282 whereby detritivore community abundance decreased on average by 49.6 % from current to future climate conditions. Similar to predators, the effects of land-use intensification on 283 detritivore communities were found to vary under current versus future climatic conditions, 284 285 such that reductions in detritivore mean abundance were significantly larger under current (55.7 % decline) versus future (34.7 % decline) climatic conditions (Table 2, Figure 3D). 286

287 Of all four trophic groups, herbivores had the highest species richness with 165 species in total. This was the only group to show significant changes in species richness in 288 response to the simulated global change, with a reduction in average herbivore species 289 290 richness of 30.2 % from low to high land-use intensity plots (Table 2, Figure 3F). 291 Furthermore, detritivore evenness increased significantly from the current to future climate scenario (Table 2, Fig. 3L). We also found a marginally significant increase in herbivore 292 293 species evenness (P = 0.052) from current to future climate treatments, but no discernible influence of land-use intensification on herbivore evenness (Table 2, Figure 3J). While 294 295 detritivore evenness showed a significant increase with land-use intensification and from current to future climate treatments (Table 2, Fig. 3L), predator and omnivore evenness were 296 297 not affected by either of the global change drivers (Table 2, Figure 3I & K). Of particular 298 note, omnivores appeared to be completely unaffected by both global change drivers, as we 299 found no significant shifts in abundance, species richness, or evenness.

300

301 3.3 Shifts in community composition

302 We found that community composition was significantly affected by both climate change and land-use intensification (Table 3, Figure 4A), though effects of land-use intensification were 303 clearly stronger than effects of climate change for the overall arthropod communities. While 304 305 significant differences in community composition between current and future climate treatments were also found, these differences were negligible in comparison to those found in 306 response to land-use intensity (Table 3, Figure 4A). Hence, communities sampled from the 307 308 same land-use intensities but different climatic conditions were more similar than communities from different land-use intensities and different climate treatments. When 309 looking at individual species contributions to these compositional changes, the SIMPER 310

311 analysis revealed generally low and varied contributions of almost all species to community dissimilarity. The only exception was for two herbivore species, Javesella pellucida 312 (Delphacidae) and Aphrodes makarovi (Cicadellidae), that had the highest contributions to 313 mean dissimilarity between low versus high land-use intensity (5 % and 4 %, respectively; 314 Table S3) and current versus future climate treatments (5 % and 3 %, respectively; Table S3). 315 Consistent with the community-level shifts in species' relative abundances, the composition 316 317 of predator, herbivore and detritivore communities were also significantly affected by climate change and land-use intensification (Table 3, Figure 4B, C & D). Whole community and 318 319 herbivore community composition showed very similar patterns, as they were particularly strongly affected by land-use intensification with especially distinct communities in low 320 versus high-land use intensity plots, but only small differences between climate treatments 321 322 (Figure 4A & C). Similarly, predator and detritivore communities also varied significantly 323 across land-use intensities and climate treatments, though land use was, again, the most important driver of compositional change (Figure 4B & D). In line with the other metrics 324 describing communities, the only exception were omnivores, where we did not find any 325 significant effects of climate or land use on community composition (Figure 4E). 326

327

328 4. Discussion

By applying interacting treatments of climate change and land-use intensification in a fieldscale experimental grassland system, our study provides evidence that both land-use intensification and climate change appear to simultaneously and additively impact arthropod community structure. There was some evidence that the strength of future impacts of land-use intensification on arthropods will be influenced by climate change, whereby future climate reduced the impacts of land-use intensification for predatory and detritivorous arthropod

335 abundance. Under current and future climatic conditions, total arthropod abundance was significantly lower in high-intensity land use plots, which lends support to the notion that 336 land-use intensification is likely to be one of the major drivers of insect declines (Hallmann et 337 338 al., 2017; Seibold et al., 2019). Furthermore, we found significant declines in the species richness of whole arthropod communities and herbivores from low to high-intensity land use. 339 Thus, with intensification of land use and under current trajectories of climate change, future 340 341 grasslands are likely to be characterized by significantly reduced abundance and species richness of arthropod predators, herbivores and detritivores, suggesting that associated 342 343 ecosystem functions may become threatened as a consequence.

Our hypothesis that future climatic conditions would reduce overall arthropod 344 abundance was mostly supported, with clear declines at the whole community level and for 345 346 detritivores. In contrast to our findings, past empirical studies have shown increased temperature to lead to higher arthropod abundances (de Sassi et al., 2012; Robinson et al., 347 2018). However, the observed positive effects of warming in these studies were mainly plant-348 mediated, where shifts in the plant community as a result of warming increased arthropod 349 abundance. Unlike these past warming experiments, the climate change treatment in our 350 351 experiment combined a temperature and precipitation manipulation to simulate the multifaceted nature of climate change (IPCC, 2014). Therefore, it is possible that the drought 352 353 effect of the climate treatment in our experiment drove the decrease in arthropod abundance, 354 either directly by water stress or indirectly through plant-mediated drought effects that alter the availability and quality of resources for arthropod communities (Huberty and Denno, 355 2004). However, due to the multi-faceted nature of our climate change treatment, we were 356 357 not able to disentangle the partial effects of temperature and drought in this study.

358 The abundance of the whole community and of predators and detritivores decreased 359 with land-use intensification under both current and future climatic conditions. However, the

360 magnitude of predator and detritivore arthropod declines varied between the climate scenarios, with a stronger decrease in abundance from low to high land-use intensity under 361 current climatic conditions. Here, climate change appeared to limit the maximum abundance 362 363 of arthropod predators and detritivores in low-intensity land use plots due to drought and higher temperatures, which therefore constrained the potential response of these arthropods to 364 land-use intensification. Hence, arthropod predator and detritivore communities that 365 366 generally benefit from less intensive management practices show lower abundances under future climate. Altogether, this result suggests that low-intensity grasslands may act as 367 368 refuges for biodiversity (Öckinger and Smith, 2006), which could be especially threatened under future climate scenarios. Further research on the combined impacts of climate and 369 land-use intensification in non-experimental systems will be needed to determine if this 370 371 prediction holds true in real grasslands.

Arthropod abundance is typically positively correlated with species richness (Schuldt 372 et al., 2019), so we expected to find similar patterns of species richness in response to the two 373 global change drivers as for abundance. Indeed, species richness of the whole-community and 374 herbivores decreased with land-use intensification, but was not affected by climate change. 375 376 Specialist primary consumers may be limited by the presence of their preferred resource plants (Koricheva et al., 2000) and, therefore, plant diversity can limit consumer abundance 377 378 and diversity (Barnes et al., 2020; Borer et al., 2012). Furthermore, habitats with higher plant 379 diversity provide a more heterogeneous habitat structure, which promotes arthropod diversity (Schuldt et al., 2019; Thomas and Marshall, 1999). These mechanisms could explain the 380 observed decline in detritivore abundance and herbivore species richness, as plant diversity 381 382 was lower in the intensively managed grassland treatments in our study. Increased harvest frequency in the intensively used grasslands may also be a driver of decreasing arthropod 383 abundance and diversity, through direct mechanical habitat destruction and damage to the 384

arthropods (Humbert et al., 2010; Klaus et al., 2013). These plant-mediated changes in 385 herbivore diversity and detritivore abundance could indirectly affect higher trophic levels 386 (Scherber et al., 2010), which might explain the decrease of predator abundance, in addition 387 388 to mechanical damage through harvesting. Furthermore, the timing of the first harvest event plays an important role for the arthropod community; harvesting in early spring, which was 389 done in intensively used grasslands, more strongly affects the less mobile stages of insects 390 391 inhabiting the vegetation, which could explain observed reductions of population size and diversity (van Klink et al., 2019). 392

393 As environmental change likely filters for species with certain functional traits (de 394 Sassi et al., 2012), we expected a decrease in evenness with global change, with increasing dominance of species that benefit from the environmental conditions caused by land-use 395 396 intensification and climate change. Surprisingly, we found that evenness increased with climate change and that land-use intensification had no effect on the evenness of the whole 397 community. The climate change response of evenness is likely caused by the loss of 398 individuals from dominant species' populations, as we found strong declines in dominant 399 400 species with high abundances under current climatic conditions (indicated by rank abundance 401 curves; Figure S2). These dominant species can play an important role in ecosystem 402 functioning as they tend to contribute strongly to the flow of energy in the community 403 (Hillebrand et al., 2008). Under stable environmental conditions, low evenness within a 404 community could theoretically lead to higher productivity of the system, as species that are well adapted to certain conditions dominate the community (Hooper et al., 2005). However, 405 406 under changing environmental conditions, such as climate change or land-use intensification, 407 higher evenness can become beneficial due to the higher capacity to adapt to the new 408 conditions (Norberg et al., 2001). Detritivores were the only trophic group that showed a change in species evenness with climate change and with land-use intensification, which, 409

surprisingly, were positive responses. This was likely due to reductions of more abundant
species, combined with no significant losses in species richness in intensive grasslands and
future climate treatments, thereby leading to increased evenness despite no significant
changes in detritivore species richness.

Overall, the composition of arthropod communities was influenced by both climate 414 415 change and land-use intensification. Predator, herbivore, and detritivore community composition showed the same patterns as the whole community in response to climate change 416 and land-use intensification, with a consistently stronger influence of land-use intensification. 417 418 Here, land-use intensification affected both the abundance and presence of species. In particular, different environmental conditions favour different species, which likely drove 419 turnover from species that benefited from low land-use intensity to species that benefited 420 421 from or could persist in high land-use intensity systems, as well as from those that benefited from current versus future climatic conditions. Furthermore, changes in the relative 422 abundance of species (without species turnover) could have also driven the observed 423 dissimilarity among communities, whereby certain species' abundances responded negatively 424 or positively to changing environmental conditions. Interestingly, we found little evidence 425 426 that any particular species were responsible for whole-community shifts observed in response 427 to land use and climate change, as individual species contributions were generally minor and 428 varied. This result likely indicates that specific traits (e.g. trophic group) may be more 429 important than species identity for explaining responses in composition of whole arthropod communities to multiple global change drivers. In contrast to herbivores, predators, and 430 431 detritivores that all exhibited significant shifts in community composition, omnivores showed 432 no responses in community composition, species richness, evenness, or abundance to the 433 experimental global change drivers investigated in this study. The invariance of omnivores in response to the climate and land-use treatments could be due to their ability to switch among 434

different resources, thereby allowing them to compensate for rarity or loss of certain resource
components under these global change scenarios (Coll and Guershon, 2002). However, given
the generally low numbers of omnivores across our treatments, any conclusions from these
data must be made with caution and further investigation is needed to determine the
underlying reasons for these findings.

440 In real-world ecosystems that will be increasingly influenced by climate change and land-use intensification simultaneously, mechanisms such as eco-evolutionary processes and 441 adaptations, range shifts, and species invasion will strongly impact ecological communities 442 443 (Scheffers et al., 2016) and may alter them in a manner which we were not able to cover here. Due to the spatially and temporally restricted experimental design of the Global Change 444 Experimental Facility (GCEF), we were unable to account for these important aspects of 445 446 changing ecosystems. The habitats of the GCEF can only be colonized by arthropods from the surrounding species pool, which is shaped by past and current climate and land use (see 447 Figure 1). However, it allows us to study how ecological communities formed by species 448 adapted to current climatic conditions could potentially perform under different land-use 449 450 intensities and climate scenarios. It is also important to note that seasonal and inter-annual 451 variation in climatic conditions is expected to increase in the future, which will likely have profound impacts on ecosystems (Thompson et al., 2013). We only partially account for, but 452 453 do not explicitly model, temporal variability in our study, which could mean that we have 454 missed seasonal and longer-term effects of the simulated global change drivers. Nevertheless, we anticipate that the effects shown in our study may be even stronger under future 455 conditions in real-world (non-experimental) grassland systems, as climate extremes increase 456 457 in the future and the ecological filtering of local communities will have a feedback effect on 458 the species pool.

We show that under current climatic conditions, land-use intensification strongly 459 impacts arthropod species richness, evenness, abundance, and community composition. In the 460 future, however, grasslands are projected to experience a combination of climate change and 461 further intensification of land use. While climate change, alone, reduces abundances of 462 arthropods and increases evenness, we show that climate change and land-use intensification 463 cause simultaneous shifts in arthropod abundance, species richness, and species composition, 464 465 that appear to be additive in nature and will likely have profound consequences for ecosystem functioning (Cardinale et al., 2006). Under future climate scenarios, reducing intensive land-466 467 use practices will be imperative to maintain the natural supply of ecosystems services provided by arthropod biodiversity in agroecosystems. 468

469

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482

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486	
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488	ES, BCR and ADB conceived and designed the study, EHS carried out the field and
489	laboratory work, EHS, UB, BR and ADB analyzed the data, and all authors interpreted the
490	results. EHS wrote a first draft and all authors contributed substantially to the writing.
491	
492	Data availability statement
493	Upon acceptance, data will be uploaded to an online repository.
494	
495	Literature
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731	
732	Figure Captions

Figure 1. Aerial view of the experimental units of the GCEF showing two of the climate

vinits in the foreground with their five land-use treatments. The arthropod communities within

- the experimental units of the GCEF (small boxes) are assembled through colonisation from
- the regional species pool (large box) which is influenced by current climatic conditions.
- 737 (Picture modified from A. Künzelmann/UFZ; insect silhouettes from www.all-

738 silhouettes.com)

739

Figure 2. Abundance, species richness and evenness of the whole community across climate

- change and land-use intensity (LUI) treatments. Lines and asterisks indicate statistically
- significant differences between climate and land-use intensity treatments (*** p < 0.001, ** p

<0.01. * p < 0.05), derived from estimated marginal contrasts (for interpretive aid only; see
Table 1 for results from GLMMs). Colours correspond to land-use intensity treatments, with
green representing low intensity managed grasslands and orange representing high intensity
managed grasslands.

747

748 Figure 3. Abundance, species richness and evenness of predators, herbivores, omnivores and 749 detritivores across climate change and land-use intensity (LUI) treatments. Lines and asterisks indicate statistically significant differences between climate and land-use intensity 750 treatments (*** p < 0.001, ** p < 0.01. * p < 0.05), derived from estimated marginal contrasts 751 752 (for interpretive aid only; see Table 1 for results from GLMMs). Lines and asterisks highlighted blue indicate a significant interaction between land-use intensity and climate 753 754 change. Colours correspond to land-use intensity treatments, with green representing low intensity managed grasslands and orange representing high intensity managed grasslands. 755

756

Figure 4. Non-metric multidimensional scaling (NMDS) plots for the whole community (A) and of the four major trophic groups, predators (B), herbivores (C), detritivores (D), and omnivores (E) based on Bray-Curtis dissimilarity. Orange polygons surround communities from high intensity grasslands and green polygons surround communities from low intensity grasslands. Solid and dashed lines denote current and future climate simulations, respectively.

Table 1. Estimates, standard errors and p-values from the generalised linear mixed effects models with whole-community abundance, species
 richness, and evenness as response variables and climate treatment ("Current" vs. "Future"), land-use intensity (LUI) treatment (low intensity
 managed grassland vs. high intensity managed grassland), and their interaction as predictors. Significant p-values are highlighted in bold.

	Abundar	ice	Species 1	Richness	Evenness		
	Estimate ± Std. Error	p-value	Estimate ± Std. Error	p-value	Estimate ± Std. Error	p-value	
Intercept	6.761 ± 0.081	<0.001	4.246 ± 0.054	<0.001	0.478 ± 0.015	<0.001	
Future Climate	$\textbf{-0.269} \pm 0.115$	0.019	-0.003 ± 0.076	0.970	0.093 ± 0.021	<0.001	
LUI High	-0.53 ± 0.094	<0.001	$\textbf{-0.189} \pm 0.08$	0.018	0.011 ± 0.018	0.570	
Future \times LUI High	0.12 ± 0.134	0.370	-0.058 ± 0.113	0.611	-0.042 ± 0.026	0.137	

Table 2. Estimates, standard errors and p-values from the generalised linear mixed effects models with abundance, species richness, and

evenness of the four trophic groups as response variables and climate treatment ("Current" vs. "Future"), land-use intensity (LUI) treatment (low
 intensity managed grassland vs. high intensity managed grassland), and their interaction as predictors. Significant p-values are highlighted in

771 Intensity managed grassiand vs. high intensity managed grassiand), and then interaction as predictors. Significant p-values are inginighted in
 772 bold.

	Predators		Herbivores		Detritivores		Omnivores	
Model	Estimate ± Std. Error	p-value						
Abundance								
Intercept	5.222 ± 0.098	<0.001	5.595 ± 0.128	<0.001	4.144 ± 0.149	<0.001	4.535 ± 0.189	<0.001
Future Climate	$\textbf{-0.209} \pm 0.139$	0.134	$\textbf{-0.234} \pm 0.181$	0.196	$\textbf{-0.798} \pm 0.220$	<0.001	-0.113 ± 0.267	0.671
LUI High	$\textbf{-0.602} \pm 0.054$	0.000	$\textbf{-0.154} \pm 0.151$	0.309	$\textbf{-0.814} \pm 0.099$	<0.001	$\textbf{-0.155} \pm 0.268$	0.562
Future Climate × LUI High	0.206 ± 0.079	0.009	-0.004 ± 0.214	0.986	0.388 ± 0.164	0.018	0.17 ± 0.379	0.654
Species richness								
Intercept	2.721 ± 0.115	<0.001	3.714 ± 0.070	<0.001	2.104 ± 0.156	<0.001	1.686 ± 0.192	<0.001
Future Climate	0.064 ± 0.160	0.690	0.019 ± 0.098	0.844	$\textbf{-0.248} \pm 0.236$	0.293	$\textbf{-0.038} \pm 0.275$	0.891
LUI High	$\textbf{-0.141} \pm 0.168$	0.402	$\textbf{-0.293} \pm 0.107$	0.006	0.000 ± 0.221	1.000	0.071 ± 0.267	0.789
Future Climate \times LUI High	0.09 ± 0.232	0.696	-0.137 ± 0.153	0.372	0.000 ± 0.334	1.000	$\textbf{-0.034} \pm 0.383$	0.930
Evenness								
Intercept	$\textbf{-0.17} \pm 0.029$	<0.001	-0.351 ± 0.023	<0.001	-0.335 ± 0.042	<0.001	$\textbf{-0.201} \pm 0.037$	<0.001
Future Climate	$\textbf{-0.007} \pm 0.041$	0.859	0.067 ± 0.032	0.052	0.148 ± 0.060	0.026	0.066 ± 0.053	0.234
LUI High	$\textbf{-0.04} \pm 0.029$	0.208	0.002 ± 0.028	0.940	0.16 ± 0.060	0.017	$\textbf{-0.098} \pm 0.046$	0.064
Future Climate \times LUI High	$\textbf{-0.013} \pm 0.041$	0.755	-0.011 ± 0.039	0.787	$\textbf{-0.09} \pm 0.085$	0.305	$\textbf{-0.018} \pm 0.064$	0.788

- **Table 3.** Results (R^2 and p-values) from permutational analysis of variance models testing for
- the effects of climate treatment and land-use intensity (LUI) under different climate scenarios
- on Bray-Curtis dissimilarity of whole arthropod communities and individual trophic groups.
- 777 Significant p-values are highlighted in bold.

	Community R ² (p-value)	Predators R ² (p-value)	Herbivores R ² (p-value)	Detritivores R ² (p-value)	Omnivores R ² (p-value)
Climate	0.08 (0.004)	0.08 (0.004)	0.06 (0.004)	0.12 (0.020)	0.02 (0.208)
LUI	0.42 (0.002)	0.13 (0.002)	0.52 (0.002)	0.17 (0.002)	0.17 (0.079)
Climate × LUI	0.04 (0.377)	0.05 (0.252)	0.05 (0.294)	0.037 (0.632)	0.004 (0.979)

- We experimentally test for combined land-use and climate change impacts on arthropod communities
- Land-use and climate change reduced total abundance and diversity, but increased arthropod evenness
- Climate change interactively reduced land-use impacts on predator and detritivore abundance
- Land-use intensity had more widespread impacts on arthropods across trophic groups than climate change
- Both drivers caused shifts in species composition, within and across trophic groups

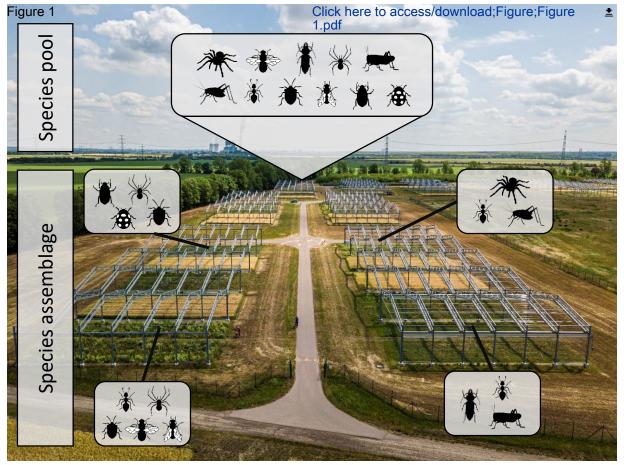
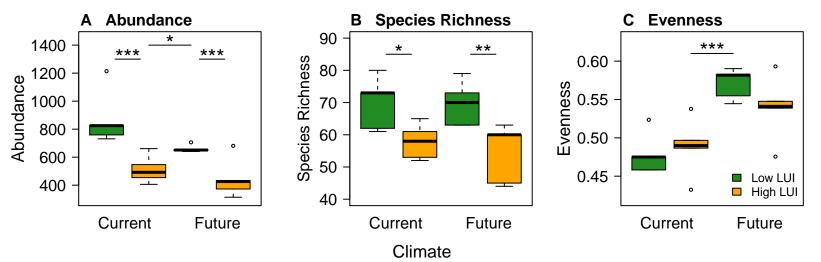
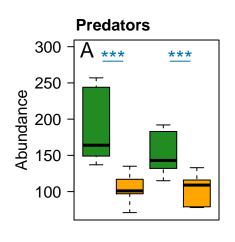
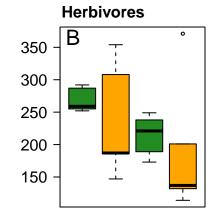


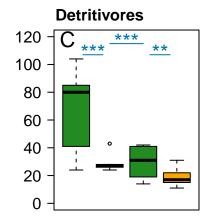
Figure 2

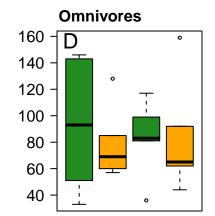
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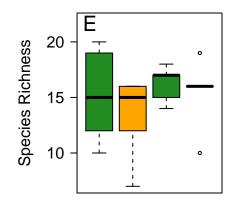


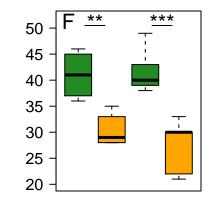


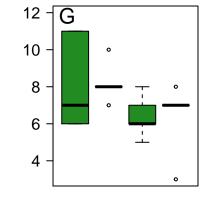


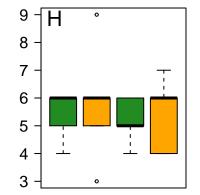


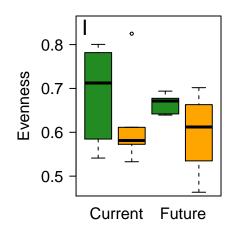


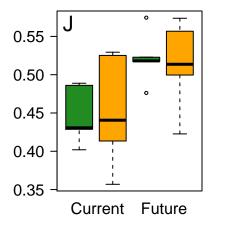


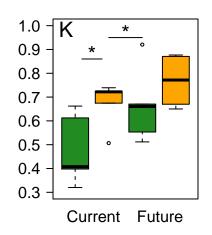


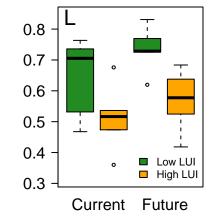








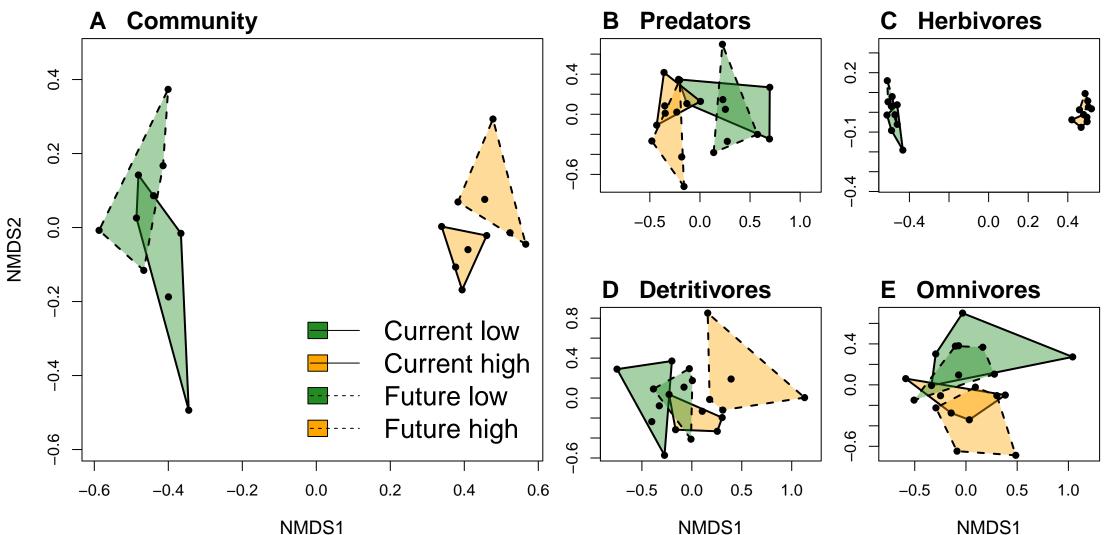




Climate

Figure 4

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1	Supporting Information
2	Esra H. Sohlström, Ulrich Brose, Roel van Klink, Björn C. Rall, Benjamin Rosenbaum,
3	Martin Schädler & Andrew D. Barnes. Future climate and land-use intensification modify
4	arthropod community composition
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6	
7	
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- 9 **Table S1.** Total abundances of each major taxonomic group collected within and across all treatments
- 10 applied in our study: low and high land-use intensity (LUI) under both current and future climatic
- 11 conditions. Taxa that were further identified by specialist taxonomists are indicated in bold.

Tayon	Current	: climate	Future	climate	Total	
Taxon –	Low LUI	High LUI	Low LUI	High LUI	Total	
Araneae	307	243	260	227	1037	
Auchenorrhyncha	772	669	547	652	2640	
Chilopoda	4	2	2	0	8	
Coleoptera	736	412	589	400	2137	
Dermaptera	4	24	4	3	35	
Diplopoda	4	0	0	0	4	
Diptera	384	456	290	299	1429	
Heteroptera	124	53	51	76	304	
Hymenoptera	977	498	726	439	2640	
Isopoda	19	9	10	15	53	
Lepidoptera	10	4	11	1	26	
Opiliones	3	1	0	0	4	
Orthoptera	2	5	6	4	17	
Sternorrhyncha	581	89	250	64	984	
Thysanoptera	600	193	638	146	1577	

12

13

- 14 **Table S2.** Abundance (Abu.) and species richness (SR) of predators, herbivores, omnivores and
- 15 detritivores across the five major taxonomic groups used in our analyses: Araneae, Auchenorrhyncha,
- 16 Coleoptera, Diptera, and Hymenoptera.

Family	Predator		Herbiv	ore	Omnivore		Detritivore	
-	Abu.	SR	Abu.	SR	Abu.	SR	Abu.	SR
Araneidae	4	2	-	-	-	-	-	-
Dictynidae	1	1	-	-	-	-	-	-
Gnaphosidae	16	NA	-	-	-	-	-	-
Hahniidae	1	1	-	-	-	-	-	-
Linyphiidae	17	16	-	-	-	-	-	-
Lycosidae	5	2	-	-	-	-	-	-
Philodromidae	1	NA	-	-	-	-	-	-
Phrurolithidae	1	1	-	-	-	-	-	-
Pisauridae	1	1	-	-	-	-	-	-
Salticidae	1	1	-	-	-	-	-	-
Tetragnathidae	2	1	-	-	-	-	-	-
Theridiidae	3	1	-	-	-	-	-	-
Thomisidae	4	3	-	-	-	-	-	-

Araneae

Auchenorrhyncha

Family	Predator	ſ	Herbivore		Omnivore		Detritivore	
	Abu.	SR	Abu.	SR	Abu.	SR	Abu.	SR
Aphrophoridae	-	-	1	1	-	-	-	-
Cicadellidae	-	-	1994	18	-	-	-	-
Delphacidae	-	-	596	7	-	-	-	-

Coleoptera

Family	Predator		Herbivo	re	Omnivore Detritivore			e
-	Abu.	SR	Abu.	SR	Abu.	SR	Abu.	SR
Anobiidae	-	-	1	1	-	-	-	-
Anthicidae	-	-	1	1	-	-	-	-
Apionidae	-	-	189	15	-	-	-	-
Carabidae	133	12			9	9	-	-
Chrysomelidae	-	-	249	18	-	-	-	-
Coccinellidae	14	4	-	-	-	-	3	3
Corylophidae	-	-	-	-	-	-	50	1
Cryptophagidae	-	-	-	-	-	-	96	6
Curculionidae	-	-	361	25	-	-	-	-
Dermestidae	-	-	-	-	-	-	1	1
Elateridae	1	1	8	1	-	-	-	-
Hydrophilidae	-	-	-	-	1	1	-	-
Latridiidae	-	-	-	-	-	-	216	5
Leiodidae	-	-	-	-	-	-	2	2
Malachiidae	-	-	1	1	-	-	-	-
Mordellidae	-	-	9	4	-	-	-	-
Nitidulidae	-	-	137	4	-	-	-	-
Oedemeridae	-	-	1	1	-	-	-	-
Phalacridae	-	_	15	4	-	_	_	-

Scarabaeidae	-	-	-	-	-	-	1	1
Staphylinidae	235	19	-	-	404	11	-	-
Throscidae	-	-	1	1	-	-	-	-

Diptera

Family	Predator		Herbivore		Omnivore		Detritivore	
	Abu.	SR	Abu.	SR	Abu.	SR	Abu.	SR
Agromyzidae	-	-	12	6	-	-	-	-
Anthomyiidae	-	-	8	4	-	-	-	-
Anthomyzidae	-	-	80	2	-	-	-	-
Biobionidae	-	-	1	1	-	-	-	-
Calliphoridae	-	-	2	1	-	-	-	-
Camillidae	-	-	4	1	-	-	-	-
Cecidomyiidae	-	-	240	NA	-	-	-	-
Ceratopogonidae	-	-	2	NA	-	-	-	-
Chaoboridae	-	-	1	1	-	-	-	-
Chironomidae	-	-	97	NA	-		-	-
Chloropidae	-	-	390	21	-	-	-	-
Conopidae	-	-	1	1	-	-	-	-
Dolichopodidae	7	1	8	2	-	-	-	-
Drosophilidae	-	-	-	-	9	1	-	-
Empididae	-	-	-	-	11	1	-	-
Ephydridae	-	-	46	5	-	-	-	-
Hybotidae	6	4	-	-	1	-	-	-
Keroplatidae	-	-	21	2	-	-	-	-
Limoniidae	-	-	1	1	-	-	-	-
Lonchopterdiae	-	-	26	2	-	-	-	-
Opomyzidae	-	-	12	3	-	-	-	-
Phoridae	2	1	-	-	39	3	-	-
Rhinophoridae	1	1	-	-	-	-	-	-
Sarcophagidae	-	-	2	1	-	-	-	-
Sciaridae	-	-	-	-	-	-	135	NA
Sepsidae	-	-	5	2	-	-	-	-
Sphaeroceridae	-	-	-	-	-	-	221	6
Syrphidae	-	-	8	3	-	-	-	-
Tachinidae	-	-	1	1	-	-	-	-
Tephritidae	-	-	2	2	-	-	-	-

Hymenoptera

Family	Predator	r	Herbivore		Omnivore		Detritivore	
	Abu.	SR	Abu.	SR	Abu.	SR	Abu.	SR
Aphelinidae	18	NA	-	-	-	-	-	-
Apidae	-	-	3	2	-	-	-	-
Bethylidae	2	NA	-	-	-	-	-	-
Braconidae	62	NA	-	-	39	NA	-	-
Ceraphronidae	277	NA	-	-	-	-	-	-
Cynipidae	-	-	8	NA	-	-	-	-
Diapriidae	109	NA	-	-	-	-	-	-
Dryinidae	1	NA	-	-	-	-	-	-
Encyrtidae	28	NA	-	-	-	-	-	-
Eucoliidae	4	NA	-	-	-	-	-	-
Eulophidae	172	NA	-	-	-	-	-	-

Eupelmidae	2	NA	-	-	-	-	-	
Eurytomidae	1	NA	-	-	10	NA	-	
Formicidae	-	-	-	-	1181	NA	-	
Ichneumonidae	51	NA	-	-	-	-	-	
Megaspilidae	7	NA	-	-	-	-	-	
Myrmaridae	211	NA	-	-	-	-	-	
Ormyridae	1	NA	-	-	-	-	-	
Platygastridae	43	NA	-	-	-	-	-	
Pteromalidae	155	NA	-	-	-	-	-	
Scelionidae	164	NA	-	-	-	-	-	
Sphecidae	2	2	-	-	-	-	-	
Tenthredinidae	-	-	6	NA	-	-	-	
Torymidae	4	NA	-	-	-	-	-	
Trichogrammatidae	4	NA	-	-	-	-	-	

19 **Table S3.** Similarity percentage analysis (SIMPER) based on comparisons for A) low versus

20 high land-use intensity and for B) current versus future climate treatments. Only taxa from a

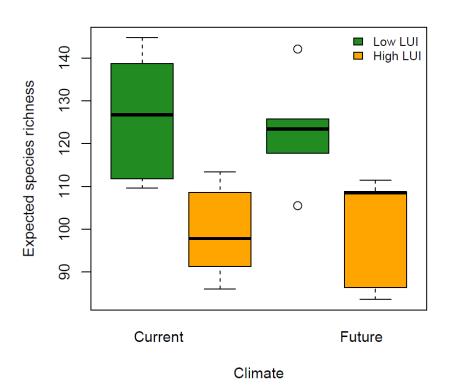
21 cumulative 50% contribution cut-off are shown.

	М	ean		Cumulative	
Species	abundances		Contribution to	contribution to	
species	LUI	LUI	mean dissimilarity	dissimilarity	
	Low	High		dissilling	
Javesella pellucida	13.70	36.60	0.05	0.07	
Aphrodes makarovi	23.70	0.20	0.04	0.12	
Megophthalmus scanicus	13.60	0.10	0.03	0.16	
Zyginidia scutellaris	0.30	13.10	0.02	0.19	
Sitona lineatus	13.50	0.90	0.02	0.22	
Atheta (Mocyta) cf. amplicollis	3.80	16.10	0.02	0.26	
Pteremis fenestralis	14.60	5.00	0.02	0.29	
Incertella albipalpis	0.30	12.10	0.02	0.32	
Euscelis incisus	12.70	1.10	0.02	0.34	
Eupteryx notata	11.30	0.00	0.02	0.37	
Anaceratagallia ribauti	10.60	0.00	0.02	0.40	
Conioscinella cf. frontella	0.20	10.60	0.02	0.43	
Tenuiphantes tenuis	9.40	12.20	0.01	0.44	
Microlestes maurus	4.00	7.80	0.01	0.46	
Anoscopus serratulae	5.70	11.20	0.01	0.48	
Protapion trifolii	7.20	0.00	0.01	0.50	

22 A) Land-use intensity

23 **B) Climate change**

	Me	ean		Cumulativa
Species	abund	lances	Contribution to	Cumulative contribution to
species	Current	Future	mean dissimilarity	dissimilarity
	climate	climate		aissiininaitty
Javesella pellucida	38.70	11.60	0.05	0.09
Aphrodes makarovi	13.70	10.20	0.03	0.13
Pteremis fenestralis	14.50	5.10	0.02	0.17
Atheta (Mocyta) cf. amplicollis	10.20	9.70	0.02	0.20
Eupteryx notata	9.00	2.30	0.02	0.22
Megophthalmus scanicus	5.80	7.90	0.02	0.25
Zyginidia scutellaris	7.60	5.80	0.02	0.28
Incertella albipalpis	4.40	8.00	0.02	0.30
Euscelis incisus	8.00	5.80	0.01	0.32
Microlestes maurus	2.60	9.20	0.01	0.35
Sitona lineatus	7.90	6.50	0.01	0.37
Tenuiphantes tenuis	10.30	11.30	0.01	0.39
Stiphrosoma sabulosum	7.50	0.40	0.01	0.41
Meligethes aeneus	6.90	2.30	0.01	0.43
Anaceratagallia ribauti	6.40	4.20	0.01	0.45
Anoscopus serratulae	8.30	8.60	0.01	0.47
Conioscinella cf. frontella	5.40	5.40	0.01	0.49
Tachyporus hypnorum	8.70	4.10	0.01	0.51



26

Figure S1. Expected species richness calculated using the jackknife 2-estimator across

climate change and land-use (LUI) intensity treatments. Colours correspond to land-use

- 29 intensity treatments, with green representing low intensity managed grasslands and orange
- 30 representing high intensity managed grasslands.

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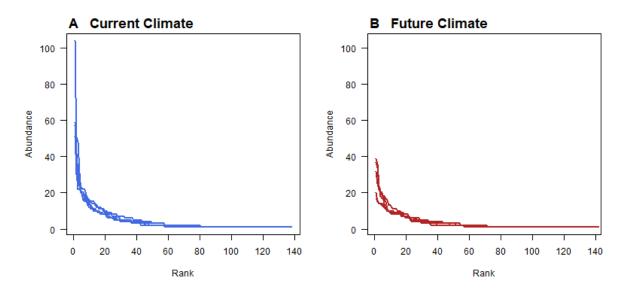




Figure S2. Rank abundance curves of the entire community within each replicate plot

34 (denoted by individual curves) under (A) current and (B) future climate treatments.

Declaration of interests

 \boxtimes The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

□The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: